

## TOWARD A NEUROETHOLOGY OF MAMMALIAN VISION: ECOLOGY AND ANATOMY OF RODENT VISUOMOTOR BEHAVIOR

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(Accepted February 3rd, 1981)

*Key words:* neuroethology – visuomotor behavior – rodent – rodent taxonomy – hamster

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### SUMMARY

The great diversity of the niches inhabited by rodents, and the variety of the visual demands of these niches, present an excellent prospect for a comprehensive neuroethological analysis of rodent visuomotor behavior. To this end, rodent taxonomy is reviewed, with special attention to the multiple independent invasions of arboreal, terrestrial, fossorial and aquatic niches by distantly related rodent species. Current work on rat, gerbil and hamster is reviewed with emphasis on visual contributions to naturalistic behaviors such as exploration, foraging, predator detection and conspecific recognition.

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### INTRODUCTION

The study of vision in rodents has had a suspect status. The laboratory rat, mouse and hamster have been viewed as simple, convenient, but regrettably underdeveloped animal models for more complex primate and human visual capacities. Thus, the study of rodent vision has been viewed as a tool for developing more powerful explanations of primate vision, but very little else. Two related assumptions underlie this 'animal model' approach. The first is that primate and human vision may be understood as an extension or elaboration on 'basic' rodent capacities: the second is that the visual capabilities of rodents are appropriately parsed using introspections loosely based on our own visual capabilities.

These two assumptions ignore so completely a basic understanding of evolutionary processes that rodent vision studied in this fashion deserves its

suspect status. Rodents diverged from the insectivores in the Paleocene epoch, at least 65 million years ago. No extant form is in any real sense 'ancestral' to primates: for example, the appearance of hominids predates the radiation of one of the most commonly studied rodent families, the cricetids (hamsters and some mice). Rodents are the most diverse mammalian order [22, 37, 47] in terms of number of species, and probably also in terms of the variety of niches they occupy. Rodents must be viewed as having evolved numerous independent neural solutions to the problems posed by a variety of visual environments.

Because of this variety in visual environments, rodents present a nearly unparalleled and as yet unexploited opportunity to study the organization and evolution of visual systems. For example, in the four major rodent subgroups, visual and visuomotor adaptations to diurnal, arboreal, aquatic and burrowing niches have been invented independently. Because of the wide range of environments and environmental rigors rodents face, they exhibit the widest range of parental investment and extent of maturation at birth of any eutherian mammal order, thus offering a natural experiment on the effects of early environment on visual system development [6, 14]. A variety of mole-like forms with regressive eyes have appeared independently, a potential rich source of information about developmental mechanisms in the atrophy and hypertrophy of sensory systems. Careful comparisons of animals from this extraordinary order should give clear answers to questions about commonalities and divergences of neural solutions to repeatedly encountered visual challenges. Though the goal of this enterprise is clearly not to provide a 'rodent model' for primate vision, paradoxically it may produce a better set of tools for understanding primate visual capacities.

This comparative approach has proved quite powerful in a variety of contexts. In bats, the typical habitat and prey type of several species has been directly related to the nature of the localizing call emitted and the properties of its neural analyses [43]. In frogs, the natural diversity of mating calls and habitats has allowed a fascinating neurophysiological analysis of a vertebrate auditory communication system [2]. The neuroethological approach to vision in anurans of Ewert, Ingle, and others has been highly productive and will serve as a partial model for this review [11, 20, 23].

Levels of neuroethological analysis are many, including analysis of the system requirements to detect or produce a particular signal in a particular environment, investigation of the neural structures required for a particular behavior, and a study of neurophysiology cast in terms of detection and response to behaviorally relevant stimuli. This review will deal primarily with preliminary studies of the role of particular neural structures in changing visual and visuomotor repertoires. We hope, however, that this analysis will raise questions for the neurophysiology of changing visual capacities.

We will first briefly review what is known about the phylogeny of the

rodents, and the relationships of extant groups. Next, examples of pairs or groups of animals that have independently invaded similar niches will be discussed with emphasis on the visual and visuomotor adaptations required, with suggestions about the use of these groups for developing a comprehensive neuroethology of rodent vision. Finally, we will review what is now known of rodent visual functional neuroanatomy in the context of this comparative neuroethological approach, with emphasis on the interdependence of visuomotor and perceptual capabilities.

#### RODENT PHYLOGENY

As an order, the rodents exceed all other mammalian orders not only in the number of individuals, but more importantly in the variety and number of forms that have evolved. Because of the sheer numbers of species the classification of the order has always been difficult. The classification problem is further complicated by the parallel evolution which has occurred within the groups and the comparatively poor fossil record which exists. As a result, any classification to date has been tentative, as is any description of the phylogeny of the various families. Nevertheless, some general agreement on classification has been reached.

Past efforts [44] have grouped the order into three major subgroups – the Sciuromorpha (squirrel-like forms), Myomorpha (mouse-like forms), and the Hystricomorpha (porcupine-like forms). This system was found to be inadequate for describing the rodent phylogeny [48, 51], especially for the diverse group of South American rodents which had been assigned to the Hystricomorpha. Specifically, it was not clear if the South American forms (e.g. guinea pigs, chinchillas) and the Hystricomorpha arose independently of each other or shared a common ancestral group. Recent evidence suggests the latter, that a common ancestral group unites the two, but that the South American forms were separated during the Eocene and underwent an extensive radiation quite independently [21]. Their classification as a separate subgroup, the Caviomorpha, results in a four-group system, a variant of which will be used here (Fig. 1). Development of a firmer classification for the order must wait for a more complete description of as yet undiscovered fossil forms which will allow the familial relationships and origins to be traced.

In many ways, the rodents have remained unchanged from their primitive mammalian ancestors (e.g. scaly coat, short legs, overall body shape) [21]. The most significant changes have occurred with the skull and dentition, which have undergone extensive alteration. The oldest animals with rodent features are classed as the family Paramyidae and arose on the North American continent over 60 million years ago during the Paleocene epoch [49]. The Paramyidae were probably direct descendants of an insectivore stock, but these original

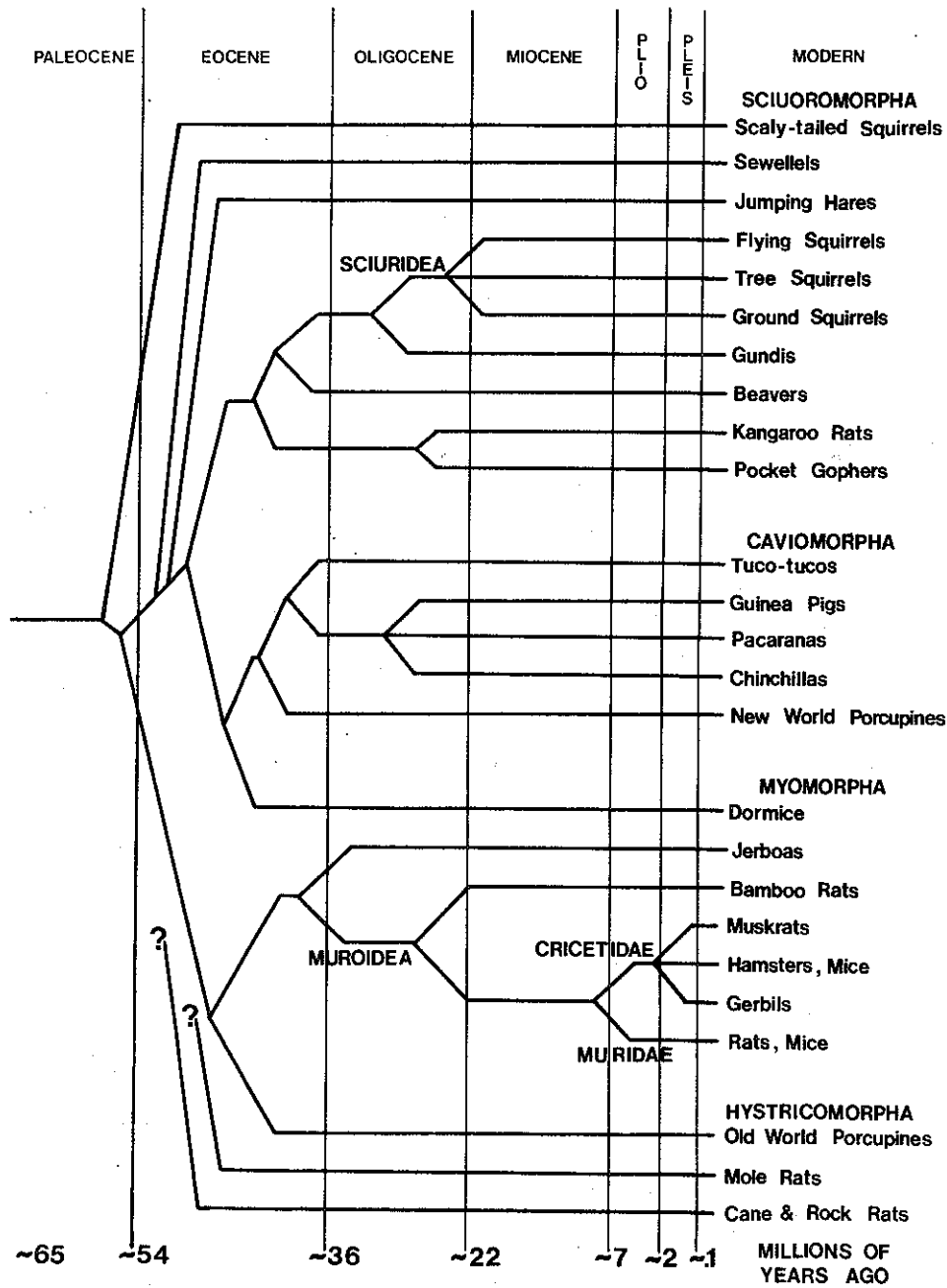


Fig. 1. Suggested phylogeny and classification of the rodents. The evolution of the rodent superfamilies with some superfamilies expanded to illustrate the phylogenetic relationships of forms mentioned in text. Representative animals of each line are listed under the four groups of modern rodents.

rodents were squirrel-like in appearance and had true rodent dentition. They were likely nocturnal, and teeth specialized for gnawing indicate that vegetation

was a likely food source. No representative of the group survives today as the line became extinct during or soon after the close of the Eocene epoch.

As gnawing mammals the Paramyidae quickly expanded, replacing any competing forms (e.g. the multituberculates) by the end of the Eocene epoch [50]. The Paramyidae underwent an extensive radiation and filled a variety of niches during the Eocene, giving rise to all of the major rodent types by the end of the epoch [49]. These groups quickly established themselves throughout the world with still further diversification during both the Oligocene and Miocene epochs. The latest groups to appear belong to the suborder Myomorpha and like most evolutionarily young groups they are extremely diverse. The youngest of all the rodent groups is the family Cricetidae (e.g. hamsters, gerbils, and some mice) which developed as recently as the Pleistocene epoch. The Cricetidae mostly inhabited central and western Europe and underwent significant modification with the climatic and accompanying habitat changes brought on during the Pleistocene ice age [52].

The next youngest rodents are the family Muridae (e.g. rats) and are closely related to the Cricetidae, having diverged from their line as recently as the early Pliocene. The Muridae proliferated in southern Europe and Asia, Africa and Australia, occupying a niche similar to that of the Cricetidae. They underwent an extensive adaptive radiation during the Pleistocene epoch as well, developing a variety of forms that exceeds that of the Cricetidae [52]. It is because of these species (the mice and rats) that the Myomorpha continues to be a flourishing group [37].

From a comparative standpoint it is interesting to note that the vast majority of ethological, anatomical and physiological studies have been done not only on the (evolutionarily) youngest members of the order but mainly on two families (the Muridae and the Cricetidae) within the same superfamily (the Muroidea). These families are therefore closely related phylogenetically and show striking similarities morphologically. Furthermore, they all fill similar niches, i.e. typically nocturnal and terrestrial or semi-fossorial. All of these characteristics make any generalization to the order as a whole difficult and comparisons to other rodent forms highly constrained. The reasons behind these particular choices of animals for study are unclear but perhaps lie in that the chosen species are commonly associated with man. This serendipitous familiarization and subsequent 'domestication' of these species, especially of the rats and mice, could therefore be responsible for producing the current limited use of the members of rodent species available.

## NATURAL EXPERIMENTS IN VISUAL SYSTEM ORGANIZATION ACROSS THE RODENT ORDER

Two types of comparisons of species are possible given the rodent diversity. Firstly, phylogenetically close relatives with markedly different visual system requirements can be compared. This type of comparison is the most powerful for highlighting those changes in neural structure accompanying a particular behavioral change. Secondly, distantly related rodent groups that have converged on similar niches can be compared. This comparison would give some indication of the variety (or similarity) of solutions to particular evolutionary problems.

*Phylogenetically close animals in different niches*

Comparisons of this first type are easy to find among the rodents. Two such examples can be found among familiar forms – the Sciuridae (squirrels) and the Cricetidae (hamsters, gerbils, voles and some mice). The Sciuridae family contains about 50 genera and are found the world over. Most species are diurnal [47] and have good visual acuity. Their diet consists of seeds, nuts, shoots and an occasional insect. This family is found in a wide variety of habitats: arboreal (e.g. 'flying' squirrels and the less dramatic tree squirrels), terrestrial (e.g. chipmunks and ground squirrels) and semi-fossorial (e.g. prairie dogs).

There are many differences in the visual demands of arboreal and semi-fossorial habitats: flying and tree squirrels are under stronger pressure for the accurate estimation of distance and depth; visual search and foraging strategies would be quite different for the nut and seed eating squirrel than the grass eating prairie dog; a great deal of prairie dog vigilance is directed to the detection of avian and terrestrial predators, while tree and flying squirrels, like other arboreal animals, are not exposed to as problematic a set of predators. The visual and visuomotor adaptations necessary for these particular problems have never been systematically described.

The Cricetidae offer more genera for comparison (approximately 100). The Cricetidae are mostly nocturnal or crepuscular and display a diversity even greater than the Sciuridae, adding semi-aquatic forms to the list of arboreal, terrestrial, and fossorial. Their methods of locomotion are quite varied, including running, hopping, climbing, digging and swimming. The gerbil (*Meriones*) and the hamster (*Mesocricetus*) are two from this group about which a fair amount is known. While they live in similar environments and exploit similar food sources, the speed and type of locomotion in these two species is quite different, as is the degree of development of their visual systems. These animals will be discussed briefly in the final section.

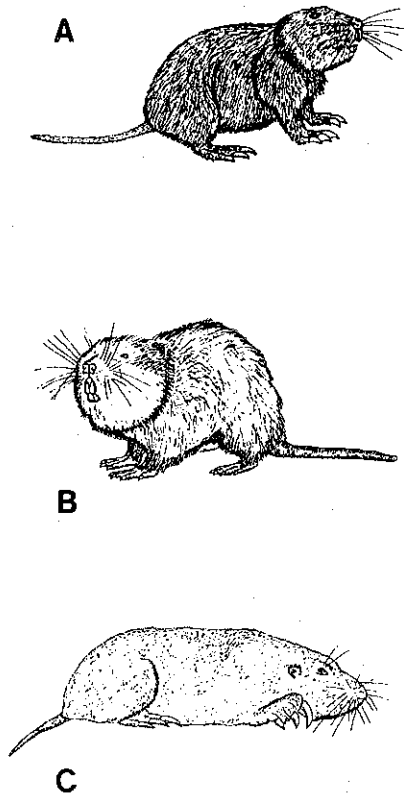


Fig. 2. Convergence of burrowing rodents. A: tuco-tuco (Caviomorpha, genus *Ctenomys*). B: bamboo rat (Myomorpha, genus *Rhizomys*). C: pocket gopher (Sciuromorpha, genus *Geomys*).

#### *Phylogenetically distant animals in similar niches*

Distantly related rodents occupying similar niches are also easy to discover. We will compare representatives of fossorial, semi-fossorial, arboreal and aquatic niches.

The fossorial forms from 3 of the major suborders have major morphological and behavioral similarities despite evolutionary distance (Fig. 2). Pocket gophers (Sciuromorpha, genus *Geomys*), tuco-tucos (Caviomorpha, genus *Ctenomys*) and bamboo rats (Myomorpha, genus *Rhizomys*) have been evolutionarily distinct forms since the Eocene epoch, i.e. over 50 million years. All three spend most of their lives underground in extensive burrow systems eating roots, tubers and the like. The morphological similarity between them is extraordinary. All have stout, thick bodies with loose skin and lack obvious necks. Their legs are short and powerful, equipped with large digging claws. Their tails are all short, thick and probably (as in *Geomys*) sensitive to touch for use when moving backward in the burrows. Their eyes and ears are quite small. The tuco-tuco probably has the best vision of the three and it spends the

most time above the ground. The eyes of the tuco-tuco are very high on the head, a position which reportedly allows the animal to scan for predators without leaving the relative safety of its burrow entrance. The questions to be asked of this group are numerous. All of these forms have regressive visual systems relative to their stem ancestor, and it is not known what uses of vision have been retained. Whether these animals retain any sensitivity to relative depth or use visual cues to designate the location of food or a burrow entrance would be first questions. A principle use of vision might be response to visual threat and modification of activity by light level. These animals might provide some information of the most basic organization of the mammalian visual system.

To date, the vast bulk of work on rodent neuroethology has been done on the closely related Myomorpha filling semi-fossorial or terrestrial niches. Hamsters, mice and rats are all typically nocturnal or crepuscular, omnivorous and live in burrows or under some kind of cover. They travel in quick runs, close to the ground and along edges whenever possible. With the exception of the hamster they also tend to be gregarious. It would be useful to supplement this research with animals from other groups that utilize the same niche. Two possibilities might be the common guinea pig (Caviomorpha, genus *Cavia*) and

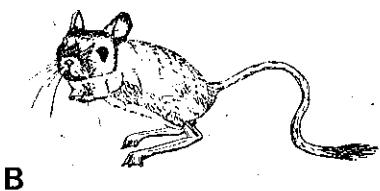


Fig. 3. Convergence of terrestrial rodents. A: kangaroo rat (Sciuromorpha, genus *Dipodomys*). B: desert jerboa (Myomorpha, genus *Jaculus*). C: gerbil (Myomorpha, genus *Meriones*).



the gundis (Sciuromorpha, genus *Ctenodactylus*). The guinea pig lives in burrows, is gregarious and feeds at night on many kinds of vegetation. The gundis lives in rock crevices on rocky slopes in small groups and, like the above, is nocturnal and feeds on many types of plants. Both the guinea pig and gundis have short legs and run with their bodies close to the ground. The generality of exploration, foraging, prey capture and visually-guided locomotion strategies described for the hamster and rat can be investigated with these animals.

Another example of convergence from distantly related groups can be found with animals like the gerbil (Myomorpha, genus *Meriones*) (Fig. 3). These typically inhabit arid country, are nocturnal, and have large eyes. They travel rapidly by hopping on elongated hind legs, feeding on plant parts, seeds, and an occasional insect. This description also fits the kangaroo rat (Sciuromorpha, genus *Dipodomys*), evolutionarily distinct from *Meriones* for over 50 million years. It also describes the jerboa (Myomorpha, genus *Jaculus*) which branched off the line which eventually produced *Meriones* about as long ago. These animals have at least two characteristics which make them interesting candidates for visual comparisons. Firstly, saltatory locomotion places high demands on depth and distance judgements. Secondly, the inclusion of insects in the diet requires specialization for rapid prey capture and tracking [23].

A comparison of arboreal climbing rodents (Fig. 4) could include the familiar tree squirrels (Sciuromorpha, genus *Sciurus*) and several long-separated Myomorpha: tree dormice (genus *Dryomys*), African climbing mice with their semi-prehensile tails (genus *Dendromus*) and vesper rats (genus *Nyctomys*). All

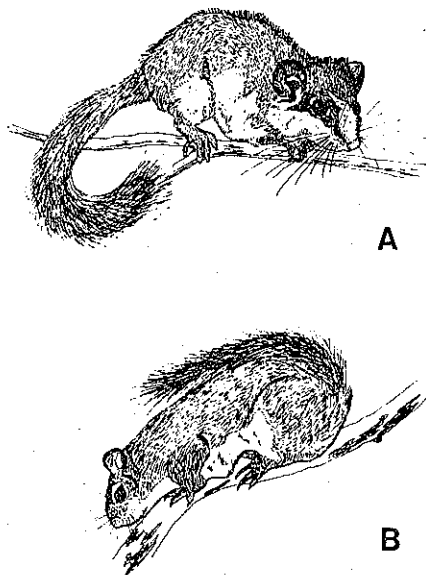


Fig. 4. Convergence of arboreal rodents. A: tree dormouse (Myomorpha, genus *Dryomys*). B: tree squirrel (Sciuromorpha, genus *Sciurus*).

are highly visual and have large eyes. They spend most of their lives in trees and are quick and agile climbers. The requirements for rapid travel through the branches would be similar for all of these rodents and a further comparison to slow arboreal climbers (e.g. prehensile tailed porcupines, Caviomorpha, genus *Coendou*) might be interesting. The specialization for color vision of the Sciuridae [31] might be compared with vision in dormice and climbing mice; it is not known if color vision appears in these groups, and what particular advantage color vision confers on the Sciuridae.

The suborder Sciuromorpha contains several types of 'flying' squirrels which can be classified into two groups – the Pteromyinae ('flying' squirrels) and the Anomaluridae (scaly-tailed squirrels). These have independently evolved from a non-flying common ancestor from the Paleocene. Like the other squirrels these have good vision and large eyes but, unlike other squirrels, are nocturnal. They both are somewhat gregarious, make their nests in hollow trees, and feed on nuts, bark and insects. They are rapid and sure-footed climbers and propel themselves into space, gliding to a designated target on the flight membranes which stretch between their limbs. It should be noted that the Anomaluridae are not closely related to the Pteromyinae; their similarity is merely the result of adaptation to similar environments.

A final comparison of a very unique group of rodents, the semiaquatic forms, might also be made. The two most familiar forms, the beaver (Sciuromorpha, genus *Castor*) and the muskrat (Myomorpha, genus *Ondatra*) are highly adapted for their aquatic life. Both have large webbed hind feet for swimming and specialized tails, the muskrat's being flattened laterally for use as a rudder and the beaver's shaped like a paddle. Typical of aquatic species, the eyes of the muskrat and beaver are positioned higher on the head. The beaver's eyes are further adapted by having nictitating membranes employed underwater. Both of these rodents build extensive structures with underwater access. The beaver is completely herbivorous while the muskrat is an omnivore. One aquatic rodent has adapted to a predacious lifestyle, the aquatic rat (Myomorpha, genus *Ichthyomys*). The aquatic rat's head is streamlined and it has small highly set eyes and small ears. The hind feet are broad and webbed for swimming. The aquatic rat spears prey (fish) with its modified gaff-like incisors. If these animals use vision underwater, which seems particularly likely in the case of the aquatic rat, the morphological or physiological methods by which they compensate for the different refractive indices of air and water would be quite interesting.

#### FUNCTIONAL NEUROANATOMY OF RODENT VISION: WORK TO DATE

The classic studies of Lashley [26–30] were paradigmatic for subsequent studies of rodent and mammalian vision, both in terms of apparatus and

guiding theory. A variety of essentially untested assumptions have characterized the literature [7]: (1) that vision in mammals may be understood as a hierarchy of more and more complex pattern perception skills, the most primitive of which is a capacity for detection of total luminous flux; (2) that 'pattern vision' (versus luminous flux detection, ambient vision, orientation to place, etc.) is a natural category of vision; (3) that various perceptual functions, such as acuity, pattern detection and form analysis may be dissociated from the response mode, such as optokinetic nystagmus or jumping stand performance, employed to show evidence of them.

The view supported here is that visual capabilities are a series of adaptive solutions to particular behavioral problems in which vision plays a role; such as food getting, recognition of same-species members, locomotion through particular environments and so forth. Evolving naturally from this view is that 'perceptual' and visuomotor capabilities must be intimately related, and should be considered together.

This review will be limited in scope, both because work in this vein has only begun recently, and because of the close evolutionary and ecological relationships of the animals that have been studied. These animals are the rat (*Rattus norvegicus*), a nocturnal, terrestrial generalist; the hamster (*Mesocricetus auratus*), a solitary, nocturnal, principally granivorous and burrowing animal; and the gerbil (*Meriones unguiculatus*), also burrowing and nocturnal, having saltatory locomotion and granivorous and insectivorous. Other work on guinea pig (*Cavia*) and mouse (*Mus*) and ground squirrel (Sciuridae) has been done, but not of a systematic nature. Even given this limited opportunity for ecological and phylogenetic comparisons, some interesting research possibilities have developed.

*Food-related activities: exploration, foraging, prey and food recognition, capture and tracking*

Curiosity and exploratory activity are one of the first behavioral characteristics of rodents noted in any general survey. The amount of this general curiosity should vary with the animal's niche, in particular with the type of predators encountered and availability and distribution of food sources. Rodents do vary in amount of open field exploration: for example, chinchillas enter and explore open arenas eagerly, rats a moderate amount, and guinea pigs hardly at all [16], but there has been no attempt to relate this to demands of exploration in the animal's natural habitat.

Open-field activity is a routine assessment for rats, mice and hamsters in a variety of experimental contexts. It is related, though not identical, to 'exploration' and 'curiosity'. The rate of open-field locomotion in all rodents studied is affected by both light level and the integrity of various central nervous

system structures related to vision [12]. Not unexpectedly for these nocturnal rodents, the amount of general activity increases markedly in the dark. This activity change normally has a circadian rhythm, but is dissociable from it.

Damage to striate cortex reduces open-field activity in hamster [42] while damage to the midbrain tectum in both rat [15, 32, 36] and hamster [12] increases activity, though not 'exploration'. Colliculus-ablated hamsters have elevated activity rates relative to normal in both light and dark; that is, they still respond to reductions in light intensity with a heightened activity rate. In rats, while average running speed is not altered [34] the form of locomotion is: they fail to inhibit ongoing activity to inspect or make choices in visual discrimination [15]. Hamsters with tectal ablations fail to show the spontaneous stopping and rearing characteristic of normal ambulation [33].

Foraging behavior is highly structured in the normal hamster; they will gather seeds [25] and crickets [13] using a highly efficient path after very brief experience. In these experiments, all seeds and crickets are in the hamster's view. Efficiency in gathering these foods is highly disrupted by tectal lesions. 'Place memory' is highly developed in the rat, multi-modal in nature, and dependent on the hippocampus [35]. A comparative study of both foraging efficiency and place memory in rodents exploiting variously distributed food sources would be highly interesting. To date, however, experimental situations are so different that meaningful comparisons cannot be made.

On entrance to an open area, normal hamsters will stop and direct their 'gaze' to at least two different positions approximately half of the time [33]. If a visual discrimination is required, scanning occurs on 80% of such entrances [33]. Hamsters without superior colliculi show very little of this behavior; their head turns usually do not exceed 10–20° while the average amplitude turn of a normal hamster required to inspect a 360° arena is 50–60°. This visuomotor loss can be associated with a variety of deficits in detection of apertures, seeds, crickets and potential predators in their posterior visual field [13]. A similar effect has been shown in rats; rats with collicular ablations show increased approach error rates if the visual stimulus for a response is physically distant from the response site, which would require sequential orienting or attending responses [32].

Direct orienting to small objects is also disrupted after tectal lesions in hamsters [41], particularly in the visual periphery [33]. In the naturalistic situation of cricket capture, this posterior visual field deficit is reflected particularly in difficulties in reorientation to and pursuit of escaping crickets, while initial approach is unimpaired [13]. A particularly interesting capability, predictive tracking of moving objects, has been shown in gerbil, and depends on striate cortex [23]. Gerbils do use insects as a food source, and this capability would be useful in natural predation. The ability to do predictive tracking has not yet been shown for any other rodent, and its development with preferred

food source would be particularly interesting.

Entirely unexplored is the question of visual recognition of food. Hamsters quickly approach seeds and edible insects after minimal experience and fail to approach the same when blinded. It is not known if certain types of visual configurations have a privileged status for recognition as food and, if there is some special recognition system, how it varies with the animals preferred food source. There is of course a major literature on learned food choice in rats, which will not be reviewed here, but little of this is concerned with the visual specification of food. In gerbils, the ability to do a variety of visual and multi-modal discriminations has been demonstrated [1, 3], but these observations have not yet been related to natural discriminations made by the animal.

#### *Surface, height and barrier*

A large literature on the visual cliff performance of rats, hamsters and guinea pigs exists, directed toward the questions of what experience is required and what central nervous system structures are required for normal performance [4, 25, 30, 33, 39, 45, 46]. In general, little experience is required for adult-like performance on the visual cliff, and striate cortex is primarily indicated in enduring deficits in this capacity. We have observed a transient deficit in cliff performance after midbrain damage in hamster, which we hypothesized to be related to the visuomotor deficit of loss of scanning head movements [12].

The role of visuomotor capacities in depth and distance perception has not been studied, probably since depth and distance perception is likely to be rather unspecialized in either the terrestrial rat and guinea pig, or the fossorial hamster. In particular, since rodents have laterally placed eyes, they have a more limited binocular segment than primates and carnivores. Because disparity cues are thus a less rich source of information for rodents, more emphasis is likely to be placed on visuomotor mechanisms for generating depth cues; i.e. head or body movements to generate parallax cues prior to jumping or leaping. This type of motor pattern has been observed in flying squirrels [47]; the neural substrate of this is particularly interesting, since striate cortex has been predominantly indicated in depth perception, while the midbrain has been typically implicated in control of head and body movement.

Perception and avoidance of barriers shows no deficit in hamster [13] and rats [18] after superior colliculus damage, but both species show deficits after damage to striate cortex. No other comparative work on rodents on this issue exists.

The area of visual perception of environmental layout is likely to be a particularly fruitful one for comparative studies, since rodents differ dramatically in the demands their environments place on this capacity. The independent evolution of various saltatory forms should provide an interesting

demonstration of the convergence or divergence of neural solutions to this problem.

#### *Perception of impending collision and threat*

Abruptly appearing overhead objects have been reported in the laboratory and the wild to produce alarm and escape reactions in a variety of rodents, which is quite reasonable in view of the avian predation on most rodents. Laboratory demonstrations of this in a variety of vertebrates and invertebrates are usually robust [40]. In hamsters, however, escape responses are difficult to elicit systematically [38] unless great care is taken to avoid habituation. An interesting account for this has been proposed for the gerbil [5]. Gerbils prevented from hiding or tunneling during early life later show less evidence of alarm to visual threat. This study indicates the importance of duplicating in laboratory studies, insofar as possible, the natural habitat of the rodent studied.

#### *Social interaction*

Although olfactory control of social interactions has been extensively studied in rodents, little attention has been paid to visual contributions to social interactions. A variety of observations suggest a role for vision in various social encounters in rodents [8-10]. In aggressive encounters, numerous species possess apparent mechanisms for visual change of apparent size, including side presentations, erect postures, and use of erectile manes and fur. Tails may be held in erect or extended position in aggressive encounters.

Many species show variation in color or bodily markings not clearly related to camouflage purposes. Many are sexually dimorphic; for example, the vischacha, a large South American rodent has facial markings which are strikingly different in the male and female. All of this evidence of visual communication is presumptive: no laboratory demonstrations have been done to demonstrate that the mode of transmission is in fact visual.

In hamsters, several studies have shown that the size of the black chest patch can be linked to success in aggressive encounters [19, 24]. An attempt to replicate this effect in duplicate experimental conditions with large numbers of hamsters in this laboratory failed [42]. However, hamsters did demonstrate they could recognize each other individually after a single aggressive encounter: 'loser' hamsters only briefly approached hamsters they had fought with and lost to, but would engage in a full aggressive encounter with another 'victor' hamster unfamiliar to them. The modality or modalities of this sophisticated recognition process is not known.

## CONCLUSION

A neuroethological approach has much to contribute to an analysis of mammalian vision. First, semi-naturalistic observations of visuomotor behavior can give a better sense of the variety of uses of vision. For example, in the frog the midbrain tectum has been shown to be involved rather exclusively in orientation to prey and escape from predation. In hamster and rat this whole-body orientation mechanism contributes to a much wider variety of behaviors, including exploration, scanning and visual sampling, efficient foraging and the ability to detect a wide class of objects in the visual periphery, as well as direct whole-body orientation to food. The richness of behaviors that include particular head and body movements makes clear the strong selection pressures on development of these capabilities.

Secondly, differentiation of visuomotor mechanisms can become much more sophisticated using an ethological approach, even given the limitations of necessarily crude lesion techniques. Thus, orientation to barriers during locomotion may be functionally and anatomically distinguished from orientation to particular food sources or interesting objects [17]; direct orientation to prey may be similarly distinguished from predictive tracking of prey [23].

This approach does not result in the mapping of newly defined complex functions onto particular structures. It is clearly not the case, for example, that foraging and food getting is a 'tectal function' while conspecific recognition is a 'cortical function'. Rather, components of these complex abilities appear to make use of extant substrates distributed over neural systems. However, a wider comparative base is necessary to begin to understand or infer the evolution of visual capacities.

This review has suggested a new approach to rodent vision and some potentially useful species for understanding the evolution of visual capacities. To date, even basic behavioral descriptions for some of these species do not exist, let alone neuroanatomical descriptions. The fact that the visually directed behaviors of the 'non-visual' rat and hamster are so remarkably rich indicates that further comparative study is likely to be quite profitable. Rodent diversity may prove to be a powerful tool in mapping behavioral change onto structural change.

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